A POSSIBLE MAGNOLIOID FLORAL AXIS, LOISHOGLIA BETTENCOURTII, FROM THE UPPER CRETACEOUS OF CENTRAL CALIFORNIA

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THE FOSSIL SPECIMEN described below was collected from an outcrop of Upper Cretaceous marine sediments in the foothills of the Diablo Range on the western border of the San Joaquin Valley near the central California town of Patterson. This locality, locally known as Black Gulch, has yielded numerous specimens of petrified woods (described in Page, 1967, 1968, 1970, 1973, 1979, 1980, 1981), as well as phosphatic concretions containing well-preserved pollen, spores, dinoflagellates, foraminifera, and radiolarians. According to Bishop (1970), the sampled sequence at Black Gulch is correlated with zone D-2 of the foraminiferal zones established by Goudkoff (1945) and is equivalent to the Ragged Valley Shale member of the Moreno Formation. Due to a discrepancy in opinion regarding the position of the Maastrichtian-Campanian boundary with respect to the foraminiferal zones of Goudkoff, there is a lack of agreement as to the age of the D-2 zone, and hence of the Black Gulch locality. Whereas most workers place the boundary between Goudkoff's D-2 and E zones, Bishop (*in* Chmura, 1973) stated that he believes the boundary to occur very near the D-1 and D-2 division. Since the Black Gulch locality lies within the D-2 zone, it is Maastrichtian in age according to most workers, but Campanian according to Bishop. Chmura (1973), who analyzed angiosperm pollen obtained from concretions, accepted Bishop's judgment, but Stein (1983) found that the concretions contain a typical Maastrichtian assemblage of dinoflagellates. The opinion of the majority of workers is adopted here.

The specimen is a calcareous petrifaction that measured approximately 3.5 cm in diameter and 3 cm in length before it was sectioned. Most of the tissues had been extensively altered, partly by pressure but chiefly by microorganisms, prior to fossilization. The general morphology is that of a herbaceous stem: a pith surrounded by a ring of vascular bundles and a cortex (FIGURE 1). The epidermis was not preserved. The pith is about 1.5 cm in diameter. Although much of the center has been destroyed, the cells—except for a peripheral zone of mostly small, relatively thick-walled ones—appear to have been large and thin walled. Numerous large cells averaging 102 μm in diameter occur individually in the peripheral zone; each is surrounded by small, flattened cells. Lenticular plates of sclereids are abundantly scattered throughout. As seen in longitudinal section, these plates are about 1 cm long and 0.5 cm thick. It is difficult to determine the shape of individual sclereids, for they are closely packed and variously convoluted (FIGURE 2). Some, at least, are branched,
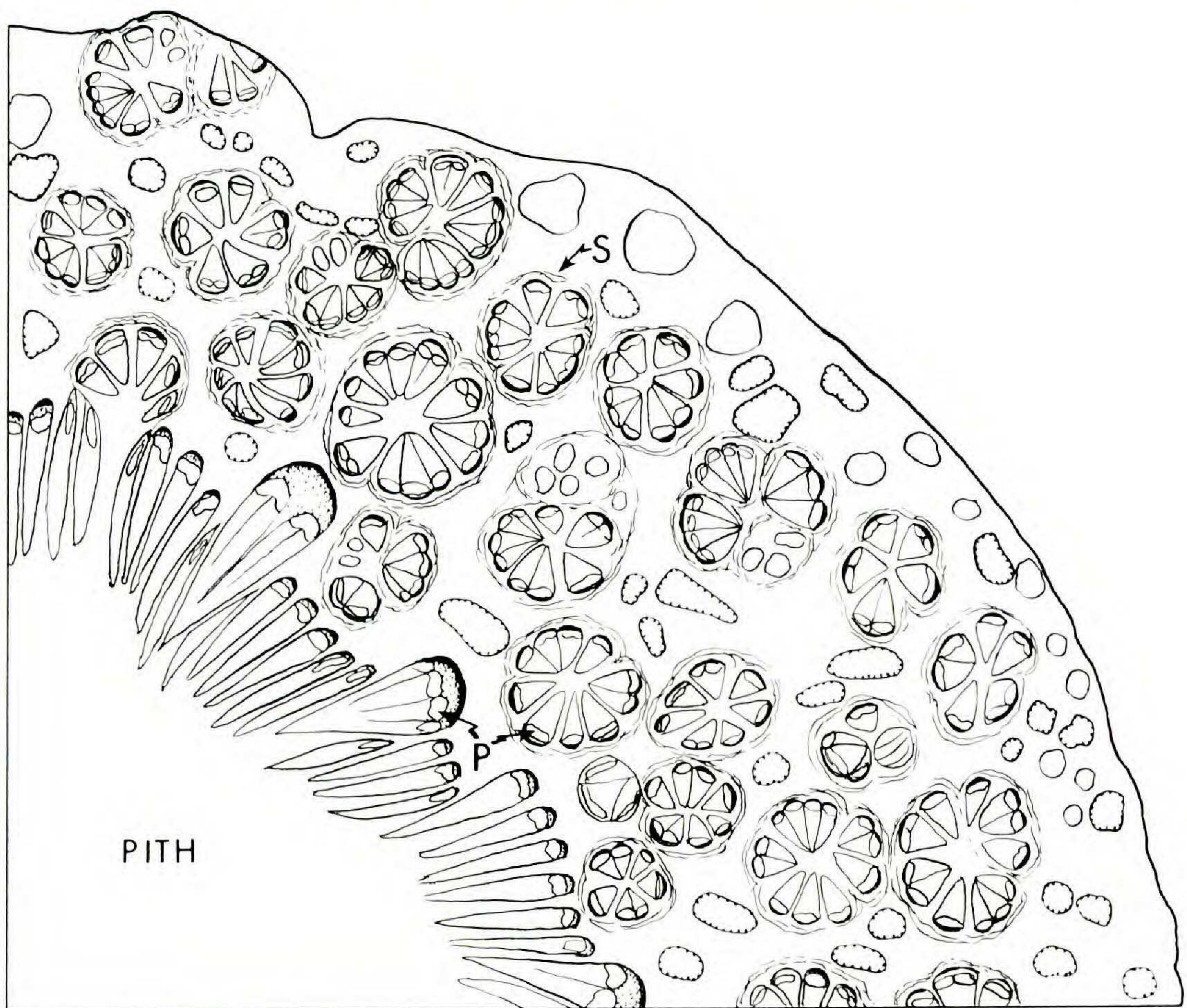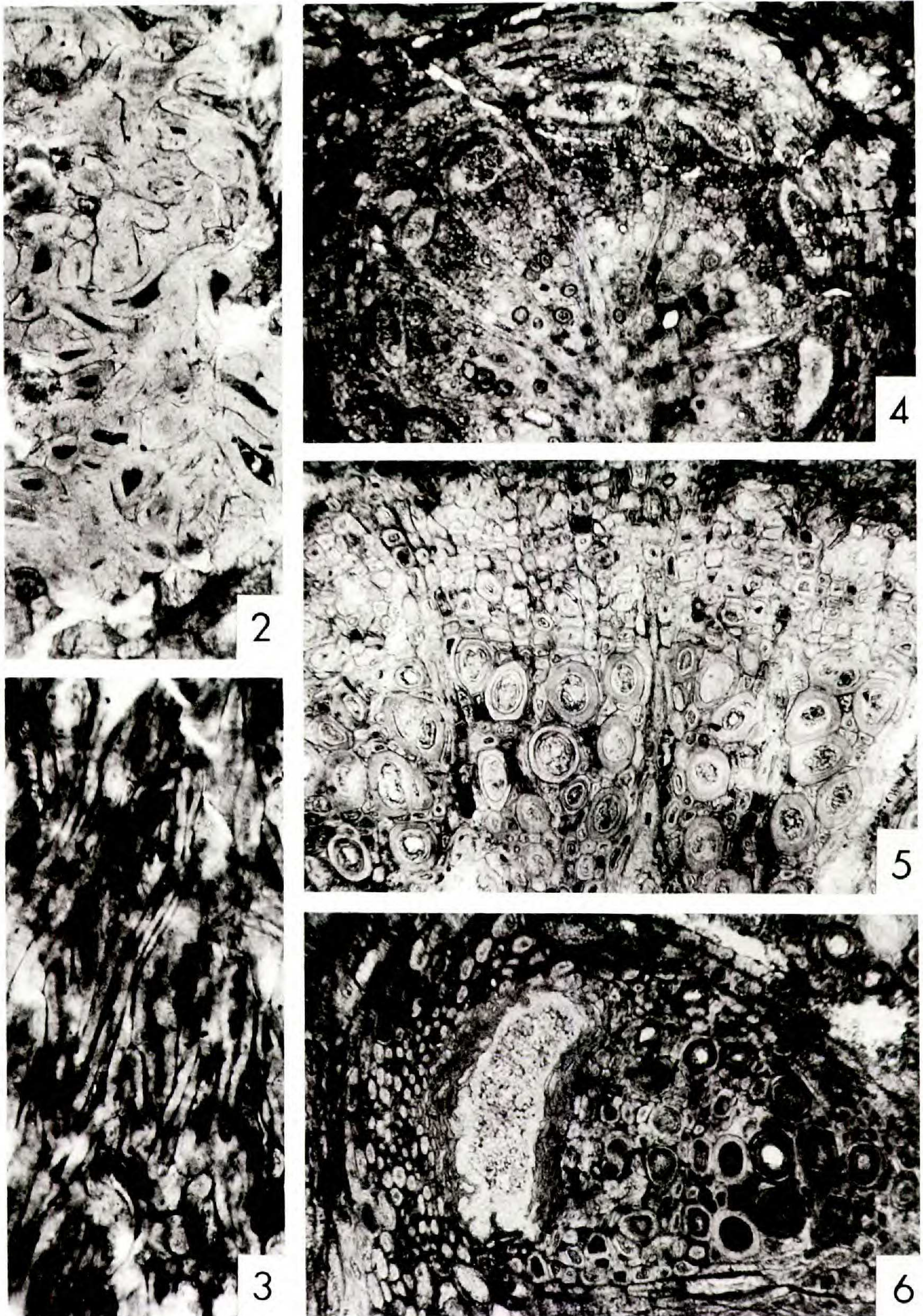
FIGURE 1. **Loishoglia bettencourtii:** diagram of quadrant in transverse section showing arrangement of vascular bundles, × 6. Those aligned at periphery of pith are stelar. Note enlarged fascicles in various stages of division and departure from stele. Stippled portions of large fascicles denote phloem fibers and crushed phloem cells. Circles of bundles in cortex show variety of patterns. Disrupted bundle circles and atrophied bundles appear as outlines, nests of sclereids as outlines with stippled borders. Pith sclereids not shown. P = phloem cavities, S = "sheath."

while others have terminal bulges. In some cases, a mass of sclereids, as seen in transverse section, lies in close proximity to a protoxylem point of a vascular bundle and extends into the interfascicular region. Individual sclereids within these masses are often elongated and lie parallel to one another (FIGURE 3). They may be as much as 300 μm in length. Although there is evidence of a cambium within the vascular bundles, there is no discernible sign of an interfascicular cambium. Metaxylem vessels are by far the most conspicuous components of these bundles. The cells are comparatively large in diameter, averaging 45 μm (range, 36–51) radially and 41 μm (28–50) tangentially, but they are less than 300 μm in length. As far as can be observed, thickening of the walls of the conducting cells of the primary xylem is exclusively spiral. It is extremely difficult to interpret the nature of the thickening in the endwalls of the conducting elements in the area of overlap between elements. David Bierhorst examined the thin sections and was able to detect areas in the endwalls

of some of the elements where the spirals were diminished in thickness and resembled bars of scalariform perforations. The nonvascular tissue of the primary xylem is composed of small cells, most of which have thick walls. Some of these cells may be parenchyma, while others appear to be fibers.

Vessels in the secondary xylem are angular, thin walled, and mostly solitary, averaging 53 μm (range, 36–57) in radial and 38 μm (21–54) in tangential diameter. The length of the vessel elements is almost impossible to measure because cell outlines are very faint; also, since the vascular bundles are seldom oriented parallel to the plane of section, few well-defined and undistorted elements can be observed. The vessel elements are, therefore, merely estimated to be about 260–360 μm long. Intervessel pits, in the few places where they can be observed, are small and opposite. Perforation plates are scalariform, with up to 20 but usually less than 10 bars. Parenchyma is sparse and occurs as single cells associated with vessels. Pits in the walls of parenchyma cells are large and lenticular. Medullary rays are heterocellular and 2 or 3 cells wide. Rays within vascular bundles are uniseriate. Thick-walled fibers with slitlike apertures make up the remainder of the nonvascular tissue. A large cavity surrounded by crushed cells occupies the presumed position of the phloem. Each bundle is capped by a group of narrow fibers.

Within the ring of numerous stelar bundles in a transverse section, as many as 15 are much enlarged. Various stages of lateral expansion of the bundles—apparently a result of radial division—can be observed. The larger of these complexes comprise several segments of primary xylem, secondary xylem, and phloem and are separated from their neighbors by bi- or triseriate rays. The enlarged bundles are displaced outwardly into the cortex, and the position they occupied in the stele is filled with parenchyma. The ground tissue of the cortex is composed of large, relatively thick-walled parenchyma cells. Nests of sclereids and large, isolated cells like those in the periphery of the pith are scattered throughout. Most conspicuous and crowded within the cortex are tight circles of vascular bundles; these are as large as 2 mm in diameter and include up to 16 bundles (FIGURE 4). Individual bundles vary in size. Most contain both primary tissue and small cells in radial files in the position of a cambium and/ or undifferentiated cambial products (FIGURE 5). Radially aligned cells are absent in smaller bundles. Except in a few cases, large cavities remain in the presumed position of the phloem (FIGURE 6). Each bundle is capped by a group of narrow fibers, and each circle of bundles appears to be bounded by a sheath of flattened cells. Possibly these latter cells were flattened by pressure exerted by centrifugal expansion of the vascular bundles. In some instances the circular arrangement is disrupted, particularly toward the outer edge of the sections. Examination of a series of four transverse sections shows that some of the bundles of a partially disrupted circle remain associated, but that others are twisting away. Fragments of bundles traverse the outer edge of the sections both vertically and horizontally. The arrangement of vascular traces in the cortex appears to be unique, for a search through the literature failed to reveal evidence of similar circles of bundles in the cortex of any structures of either monocotyledons or dicotyledons. I must point out, however, that complete anatomical studies of axes of the primary body of woody plants are very limited;

FIGURES 2–6. **Loishoglia bettencourtii**: 2, nests of sclereids, transverse section, showing convoluted pattern, × 100; 3, pith sclereids, longitudinal section, showing elongated form, × 100; 4, circle of cortical bundles, transverse section, × 37; 5, enlargement of portion of 3 contiguous cortical bundles, transverse section, showing undifferentiated secondary xylem above and primary xylem with thick-walled vessels below, × 100; 6,

studies of inflorescence axes of both woody and herbaceous plants are even more limited.

SYSTEMATIC DESCRIPTION

Loishoglia Page, gen. nov.

Axes with central cylinder of collateral bundles surrounding a pith composed of parenchyma, nests of sclereids, and isolated secretory cells, and a cortex with narrowly wedge-shaped vascular bundles arranged in numerous tight circles of up to 16 bundles per circle. Metaxylem vessels with walls spirally thickened, perforations scalariform. Vessels of secondary xylem solitary with small, opposite intervessel pits. Perforations scalariform with up to 20 but usually fewer than 10 bars. Medullary rays heterocellular, 2 or 3 cells wide.

TYPE SPECIES. *Loishoglia bettencourtii* Page.

Loishoglia bettencourtii Page, sp. nov.

Pith. 1.5 cm in diameter. Parenchyma cells large, thin walled except for peripheral zone of small, thick-walled cells. Secretory cells avg. 102 μm in diameter. Sclereids in lenticular plates 1 cm long and 0.5 cm thick in longitudinal section.

Vascular bundles. Vascular bundles numerous. Primary xylem vessels solitary, isodiametric, avg. 45 μm (range, 32–50) in diameter, ca. 300 μm long. Perforations scalariform. Secondary xylem vessels mostly solitary, avg. 53 μm (36–57) in radial diameter, 38 μm (21–54) in tangential diameter. Vessel element length ca. 360 μm. Intervessel pits small, opposite. Perforations scalariform, with up to 20 but usually fewer than 10 bars. Parenchyma sparse, occurring as single cells associated with vessels. Medullary rays 2 or 3 cells wide, heterocellular; rays within bundles uniseriate. Ground tissue of thick-walled fibers with slitlike apertures. Phloem fibers thick-walled, narrow, forming centrifugal cap as viewed in transverse section, sieve cells not preserved.

Cortex. Circles of vascular bundles numerous; individual bundles similar to those of central stele except secondary tissues undeveloped or lacking. Solitary bundles numerous at periphery. Ground tissue parenchymatous with numerous nests of sclereids. Secretory cells abundant.

MATERIAL. One calcified petrifaction measuring 3.5 cm in diameter and 3 cm in length.

HOLOTYPE. California Academy of Sciences Geological Collections no. 61208.

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individual vascular bundle, transverse section, showing primary xylem to right and cap of phloem fibers to left of large phloem cavity (note crushed cells surrounding cavity), × 70.

The genus is named after Lois Hogle in recognition of her kindness in providing transportation to the collection site. The specific epithet is in honor of the Bettencourt family of Crow's Landing, California, for allowing me to collect on their property over the years.

LOCALITY. Moreno formation. Black Gulch; NE¼, SE¼ sect. 32, R7E, T5S, Oristimba 15″ quadrangle, California.

AGE. Maastrichtian.

DISCUSSION

The specimen remained an enigma for a long time mainly because of the unusual structure of the cortex and the difficulty in determining the nature of the endwalls of the vessel elements in both the primary and the secondary xylem. The presence of a fascicular cambium is an indication that the specimen is a dicotyledon, for in monocotyledons the cambium is exclusively extrafascicular. The anatomy of the stele has characteristics of certain dicot stems. The numerous gaps left by traces in various stages of departure from the stele are suggestive of a system of much-telescoped internodes and possibly a spiral phyllotaxy such as one would expect to find either in the receptacle of a flower with numerous parts or in the peduncle of an inflorescence.

Among flowers examined, receptacles of members of the Magnoliaceae (particularly in the perianth region in *Magnolia* L. and *Liriodendron* L.) proved anatomically most similar to the fossil. In plants of both *Magnolia* and *Liriodendron*, numerous collateral bundles surround a large pith containing nests of sclereids and secretory cells. Cambial activity is minimal and confined to the vascular bundles. Sclereids and secretory cells occur in the stems of many genera of dicots, but the combined occurrence of nests of sclereids of the type observed in *Loishoglia* and secretory cells in both pith and cortex is not common and, as far as I can determine, has been reported only in certain families of the Magnoliales. Among these families, vessel elements of the type observed in the secondary xylem of the fossil are found only in genera of the Magnoliaceae. Although much larger than the secretory cells of the species of *Magnolia*, *Michelia* L., and *Liriodendron* examined, the enlarged cells of parenchymatous tissues in *Loishoglia* may be homologous with them, for they are similar in shape and distribution. In the modern forms examined these cells usually are not surrounded by flattened parenchyma cells as they are in the fossil. It is possible that the condition in the fossil is due to excessive expansion of the secretory cells early in differentiation. Although of the same general type as those in the Magnoliaceae, sclereids in *Loishoglia* tend to be much longer. The structure of the vascular elements in the fossil is consistent with that in many members of the Magnoliaceae. Scalariform perforations with less than ten bars are characteristic of vessels in the secondary xylem, and opposite intervessel pits are present in a number of genera. Vessel elements of the primary xylem range from slightly over 200 μm to 500 μm in length in the stalk and receptacle of the magnolia flowers examined. Because of poor preservation, it was impossible to measure more than one vessel in the primary xylem of the fossil.

This element, which was 290 μm long, falls in the lower portion of the range observed in *Magnolia*. However, the numerous fragments visible in longitudinal sections indicated that the average length of vessel elements was probably greater than 290 μm. The most obvious difference between the fossil and the modern forms lies in the cortex. Most of the cortical bundles in the receptacle of *Magnolia* or *Liriodendron* are single or in pairs, but occasionally a circle of three (or rarely four) occurs, particularly in *Liriodendron*. In the specimens examined (*L. tulipifera* L. and ornamental varieties of *M. grandiflora* L.) cortical bundles occurring in circles are broadly wedge shaped and arranged (as in the fossil) so that in transverse section the apices of the wedges are in juxtaposition. Parenchyma cells immediately surrounding a circle of bundles differ only slightly in shape and size, so there is nothing resembling the sheaths of flattened cells characteristic of the circles of bundles in the fossil.

If the fossil is homologous with floral axes of members of the Magnoliaceae, an explanation of the pattern of cortical traces is necessary. Two interpretations are possible. First, the specimen may represent a portion of the axis of an individual flower, and the cortical bundles traces to its various components. As noted above, occasional circles of three or four wedge-shaped vascular bundles occur in transverse sections of flower stalks and receptacles of *Magnolia* and *Liriodendron*. It is probable that these circles represent situations in which branches of traces developed parallel to one another for a short distance before diverging from the parent trace. Although more complex, the condition in the fossil may be similarly explained. The seeming complexity may stem from the more profuse branching of traces in the fossil. In sections of receptacles of *Liriodendron* and *Magnolia*, many traces diverging from the stele appear to be dividing bilaterally. In the fossil some stelar bundles appear to be dividing bilaterally, but others look as though they were undergoing multiple divisions (see Figure 1). Whereas in the modern forms these branches soon diverge, in the fossil most remain associated for at least the length of the specimen, and some are joined by a sympodium from another level of the stele. (Since the direction of provascular development is not known, trace patterns are discussed here as if they had been basipetal.)

The second interpretation, derived from Nast's (1944) description of the vasculature of the cymelike inflorescences in species of *Drimys* J. R. & G. Forster (Winteraceae), is that the specimen may have been part of the peduncle of a compound inflorescence, in which case the circles of bundles may be traces to pedicels. Nast (p. 458) stated that in the flowering stalk, "each thickened area of the stele breaks up into a number of bundles as it leaves the central cylinder and almost immediately assembles into steles of the floral pedicels. The pedicels may contain one or two concentric bundles or a cylinder of bundles." The cortical circles of bundles in the fossil, *Loishoglia*, may be homologous with the pedicel traces of *Drimys*; however, unlike the latter, which enter the pedicels at more or less the same level in the axis as they depart from the central stele, those in the fossil continued on at a much more acute angle for some distance before connecting with a pedicel. That groups of traces may have maintained a circular configuration on departure from the main axis is suggested by the presence of circles in longitudinal sections tangential to the

outermost edge of the specimen. More difficult to explain in either interpretation are the numerous individual bundles and small circles crowded at the outer edge of the cortex in transverse sections. In these bundles the cells are crushed and wrinkled as if atrophied.

Although *Loishoglia* has several anatomical characteristics in common with the Magnoliaceae, the unique vascular pattern of the cortex distinguishes it from all members of both that family and related ones. If the circles of bundles in the cortex represent incipient steles of pedicels, this would suggest that the inflorescence was complex. Although flowers of the Magnoliaceae are generally solitary, in *Elmerrillia* Dandy and *Michelia* there may be more than one per inflorescence. Moreover, there is some evidence that the flowering axes of the closest relatives of the Magnoliaceae, the Degeneriaceae and Himantandraceae, may be reduced from more complex structures. In *Galbulimima* F. M. Bailey (Himantandraceae) bracts at the base of the receptacle subtend axillary buds that occasionally develop into subsidiary flowering axes (Bailey *et al.,* 1943). The flowering axes of *Degeneria* I. W. Bailey & A. C. Sm. bear bracteoles thought by Bailey and Smith (1942) to indicate that the axes had been reduced from more complicated systems. Compound inflorescences, therefore, may have been characteristic of the ancestral group from which these families were derived.

Three wood and stem specimens showing possible affinities with the Magnoliaceae or related families have previously been described from the Maastrichtian of central California. Two of these (SUPTC[1] 10,000, *Magnoliaceoxylon panochensis* (Page) Wheeler, Scott, & Barghoorn (Page, 1970), and CASG 60425 (Page, 1980)) are fragments of secondary wood, and one (CASG 60133 (Page, 1980)) is a young stem with pith and both primary and secondary xylem. The possible relationship between the latter specimen and the Magnoliaceae was not recognized initially because its solitary pores and heterocellular rays are not typical of the family. It does, however, contain pith sclereids of the magnoliaceous type, and secretory cells are present in the rays and pith. Of the three specimens, 60133 is most similar anatomically to *Loishoglia*. It is a stem or branch 2.5 cm in diameter with a large pith 1 cm in diameter. Pores in the metaxylem are 21–43 μm in diameter; those in the secondary xylem 86–96 μm. Intervessel pits in the secondary xylem are small and opposite, and perforation plates are scalariform with less than ten bars. Secretory cells in the pith are devoid of contents and difficult to distinguish in transverse section from the very large, thin-walled parenchyma cells, but a few can be observed in the longitudinal plane where the parenchyma cells are mostly flattened. The secretory cells are comparable in size to those in *Magnolia* (avg. 80 μm) and are thus smaller than those observed in *Loishoglia*. Enlarged cells in the rays, interpreted as secretory (Page, 1980, *fig. 4*), are closely similar to such cells in the rays of secondary xylem in *Magnolia*. Pith sclereids are much like those in *Loishoglia*. An additional feature typical of the Magnoliaceae can be observed in transverse sections of specimen 60133. The sections are through a

[1]Stanford University Paleontological Type Collection, now housed at the California Academy of Sciences, San Francisco.

multilacunar node with a large median trace flanked by two small traces and eight additional lateral traces. As described by Canright (1955), the typical nodal pattern in *Magnolia* is similar except for the presence of a stipular trace opposite the median trace. Tissues in the area where a stipular trace would be expected were not preserved in the fossil; therefore, it is not possible to determine whether such a trace was originally present. Several traces are present in the fossil that are not figured in Canright's diagram. This difference may not be significant, for he has pointed out that the number of nodal traces in species of *Magnolia* is extremely variable both inter- and intraspecifically; however, although the number of lateral traces may vary from four to fifteen, the median and stipular traces are always present.

The numerous anatomical similarities observed in CASG 60133, *Loishoglia,* and stems of the Magnoliaceae suggest that the fossils were related to one another and to the Magnoliaceae. Although vessel elements in the secondary xylem of *Loishoglia* are on the average smaller in diameter than those in either 60133 or most members of the Magnoliaceae, they compare well in size with elements in the earliest-formed secondary xylem (where the vessels are about half the diameter of those in subsequent increments). Secretory cells in *Loishoglia,* however, are much larger than those in 60133 and the species of *Magnolia, Michelia,* and *Liriodendron* examined. It is possible that the two fossils were related but not necessarily derived from members of the same natural species or genus. The locality from which 60133 was collected is slightly younger than the horizon in which *Loishoglia* was found. It has been estimated (Page, 1981) that the two localities are separated by an interval of about 1.5 million years.

The two specimens of secondary wood, SUPTC 10,000 (from the same locality as *Loishoglia*) and CASG 60425 (from the same locality as 60133), are closely similar to the woods of the modern Magnoliaceae except for the absence of terminal parenchyma. They differ from each other in that the intervessel pits appear to be scalariform in 60425, whereas they are mostly opposite in 10,000. Neither specimen shows evidence of secretory cells, and since both consist only of secondary wood, no sclereids are present. Until additional material becomes available, it is useless to speculate on the relationship between these two specimens and *Loishoglia.* The lack of secretory cells in itself may not be significant; among modern species of Magnoliaceae it is not unusual for such cells to be absent from the secondary wood but consistently present in primary tissues.

The magnolialian complex can be traced at least to the early part of the Upper Cretaceous, as indicated by fruits and leaves described by Dilcher *et al.* (1976), Crane and Dilcher (1982), and Dilcher and Crane (1982, 1984) from the early Cenomanian of Kansas. When compared with modern derivatives of the ancestral complex, *Loishoglia* appears to be most closely allied to the clade consisting of the Degeneriaceae, Magnoliaceae, and Himantandraceae. *Loishoglia* and the putative magnolioid wood specimen (CASG 60133) can be added to a growing list of extinct Cretaceous genera of dicotyledons. The knowledge that a significant number of Cretaceous angiosperm genera are now extinct should be sufficient reason for caution in assessing the degree of relationship between pre-Tertiary woods and supposed modern counterparts.

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